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Dynamic networks of fighting and mating in a wild cricket population

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Reproductive success is often highly skewed in animal populations. Yet the processes leading to this are not always clear. Similarly, connections in animal social networks are often nonrandomly distributed, with some individuals with many connections and others with few, yet whether there are simple explanations for this pattern has not been determined. Numerous social interactions involve dyads embedded within a wider network. As a result, it may be possible to model which individuals accumulate social interactions through a more general understanding of the social network's structure, and how this structure changes over time. We analysed fighting and mating interactions across the breeding season in a population of wild field crickets under surveillance from a network of video cameras. We fitted stochastic actor-oriented models to determine the dynamic process by which networks of cricket fighting and mating interactions form, and how they co-influence each other. We found crickets tended to fight those in close spatial proximity to them and those possessing a mutual connection in the fighting network, and heavier crickets fought more often. We also found that crickets that mated with many others tended to fight less in the following time period. This demonstrates that a mixture of spatial constraints, characteristics of individuals and characteristics of the immediate social environment are key for determining social interactions. The mating interaction network required very few parameters to understand its growth and thus its structure; only homophily by mating success was required to simulate the skew of mating interactions seen in this population. This demonstrates that relatively simple, but dynamic, processes can give highly skewed distributions of mating success.

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Organisms engage in social interactions when they mate, fight, cooperate and compete for resources with conspecifics (Frank, 2007). Interactions such as these influence an individual's fitness and allow it to influence the fitness of others (Formica, WoodLarsenButterfieldAugatHougen, & Brodie, 2012; Royle, Pike, Heeb, Richner, & Kölliker, 2012; Wey, Burger, Ebensperger, & Hayes, 2013). Social interactions can therefore play a key role in ecological and evolutionary processes. Furthermore, these interactions are temporally dynamic, as individuals change interactions partners over time (Blonder & Dornhaus, 2011; Blonder, Wey, Dornhaus, James, & Sih, 2012). This may influence the rate at which individuals encounter potential mates or competitors, the rate of opportunities for pathogen and information transmission and the opportunities for different social strategies (Pinter-Wollman et al., 2013). How individuals accumulate social interactions is therefore key for several aspects of their fitness.

Reproductive skew in wild populations is typically substantial, with many individuals achieving no or little success, while some individuals are highly successful (Clutton-Brock, Rose, & Guinness, 1997; Engh, 2002; Frentiu & Chenoweth, 2008; Keller & Reeve, 1994; Rodríguez-Muñoz, Bretman, Slate, Walling, & Tregenza, 2010; Ryder, Parker, Blake, & Loiselle, 2009; Thompson, Hassall, Lowe, & Watts, 2011). This reflects a skew in social interactions, with some individuals having many mating connections, while most having very few or none. In fact such a skew is common across all sorts of social networks, where most individuals have few connections, while a small number of others are very well connected (Croft, James, & Krause, 2008; Krause, James, Franks, & Croft, 2014). Since both a network of social interactions and a set of mating interactions in a population arise from many dyadic interactions accumulating over time, this raises the possibility that similar processes give strong skews in mating success and social network connections. Not mutually exclusively, it is also possible that the accumulation of interactions in one context influences the interactions in the other context, so for example a high number of interactions in a grooming network leads to many connections in a mating network.

Networks with properties similar to real-world networks can be simulated by dynamic network growth models with few rules (Ilany & Akçay, 2016; Newman, 2002), indicating that a network's

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structure can be directly dependent on the dynamic processes that form it. Similarly, simple rules that individuals follow in relation to the movement of fellow group members can result in the apparently complex patterns displayed in murmurations of starlings or synchronized swimming in shoals of fish (Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015; Sumpter, 2006). Understanding individual-level decisions about interactions with other population members may therefore allow us to explain the structure and properties of whole groups, including the spread of mating interactions within a population.

To investigate these topics, we used dynamic social network analysis to explore the pattern of social interactions, in the form of aggressive dyadic contests (fights) among individually marked wild adult field crickets, *Gryllus campestris*. These interactions represent intrasexual competition. We tested the prediction that changes in the fighting network across the lifetime of an individual are not purely stochastic, and that factors expected to influence choice of opponents (such as the distance separating the dyad, or the size difference between the individuals) influence the formation of links in the network. To examine how these social interactions relate to fitness, we then looked at how a network of mating interactions (based on copulation events) changed over time and how it was influenced by and influenced the fighting network. We tested the prediction that the mating network is also not purely stochastic, and that factors thought to be important for attracting mates (such as an individual's size, or its size relative to the potential partner) and the ability to gain access to mates (such as the frequency of fighting) influence the formation of links in the network. This provides insights into how mating interactions accrue within this wild population and, hence, into the processes contributing to the large skew in reproductive success observed in this population (Rodríguez-Muñoz et al., 2010).

METHODS

Study Site

The study site is located in a meadow in northern Spain (for further information, see www.wildcrickets.org; Rodríguez-Muñoz, Boonekamp, Fisher et al., 2019; Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Fisher et al., 2019; Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen et al., 2019; Rodríguez-Muñoz et al., 2010). We used data collected in 2013 for this analysis. In the early spring we located each burrow and marked it with a unique identifier. In late April, just before adults started to emerge, we set out 124 cameras at random at burrows with an active juvenile cricket (nymph). This allowed us to record the exact moment of emergence for those adults and all subsequent behaviour at the burrows. See Table 1 for a description of the behaviours recorded relevant to the current study. We directly monitored burrows that were without cameras daily or every other day and recorded the life stage (nymph or adult) and identity of the individual (if a tagged adult) using the burrow. As nymphs only very rarely move among burrows, when there was an untagged adult at a burrow, where on the previous days there had been a nymph, we could infer the emergence date for that adult. This allowed us to record accurate emergence dates for the vast majority of the population. Adults mate with members of the opposite sex, fight individuals of (typically) the same sex and hide from predators at these burrows (Rodríguez-Muñoz, Bretman, & Tregenza, 2011), so by monitoring the burrows directly we captured the vast majority of relevant cricket behaviour. A single observer (D.N.F.) watched 89% of the videos from 2013. If we did not observe a cricket's death, we estimated it as the day after it was last observed. A few days (mean ± SD = 3.76 ± 2.81) after a cricket emerged as an adult, we trapped it (using a custom-built trap, see www.wordpress.com/crickettrapping, for more details) and transported it to a laboratory adjacent to the field site. Here we weighed it and fixed a waterproof vinyl tag to its pronotum using cyanoacrylate glue. This allowed the identification of individuals, and as far as we are aware did not affect their natural behaviour. After tagging the crickets, we released them back to the burrow from which they were trapped, which we kept blocked in the meantime to prevent other animals, including other crickets, from usurping the burrow. We moved cameras away from burrows that hosted no cricket activity for 2 days to nearby ones where cricket activity had been directly observed or which showed signs of activity. As the season progressed there were more cameras than live adult crickets. This gave us very good information on behaviours over individuals' entire adult lifetimes. Measurements of rainfall and intensity of solar radiation were taken at 10 min intervals using a weather station situation in the centre of the meadow (Vantage Pro 2, Davis instruments, CA, U.S.A.).

Study Organism

Gryllus campestris is univoltine, and adults are active during April – July following overwintering as nymphs in burrows that they dig themselves. Once sexually mature, males start calling to attract mates, and both sexes move among burrows to search for mating partners. When encountering a member of the same sex at a burrow, they typically fight, with the loser leaving the burrow (Alexander, 1961). While many male and female *G. campestris* achieve very low fitness, small males that sing frequently and larger, long-lived and more promiscuous individuals of both sexes achieve higher lifetime reproductive success (Rodríguez-Muñoz et al., 2010). In *G. campestris,* reproductive success is strongly influenced by mating success (Rodríguez-Muñoz et al., 2010), although post-copulatory processes may have some influence (Bretman & Tregenza, 2005; Bretman, Newcombe, & Tregenza, 2009, 2011). Hence the use of accumulation of mating interactions as a proxy for the accumulation of fitness is reasonable.

Modelling Dynamic Networks with SAOMs

We used stochastic actor-orientated models (SAOMs) to model the dynamic networks of mating and fighting interactions in our population of field crickets and therefore (1) determine processes that lead to network structure (and hence the skew in connections) of each and (2) determine how the networks influence each other. As connections in the mating network represent potential fitness gains, modelling how links in the mating network form over time aids our understanding of how individuals acquire fitness in the wild. SAOMs allow the modelling of the change in individuals' social interactions and behaviours over time, as influenced by individual or dyadic (depending on some aspect of the existing relationship between two individuals) effects and properties of the existing network structure (Burk, Steglich, & Snijders, 2007; Snijders, van de Bunt, & Steglich, 2010; Steglich, Snijders, & West, 2006). SAOMs can also be used to study transmission dynamics (e.g. Pasquaretta et al., 2016; Silk et al., 2017) and the effect of environmental factors on social interactions (e.g. Ilany, Booms, & Holekamp, 2015). These models are therefore useful for testing a range of hypotheses of interaction in behavioural and evolutionary ecology (Fisher, Ilany, Silk, & Tregenza, 2017). We implemented our SAOMs in the R package 'RSiena' (Ripley, Snijders, Boda, Voros, & Preciado, 2015).

Network Construction

Initially we were interested in the fighting behaviour of individual crickets. We judged two crickets to have fought if there was

Table 1
A description of each of the behaviours relevant to the current study recorded by the array of video cameras

Behaviour	Description
Leaves	A cricket leaves the area around a burrow monitored by the camera and does not return for 5 min. If the cricket is never seen again this will be its last action
Fights	Two crickets fight, by engaging in some form of aggressive interaction (e.g. charging, flaring of mandibles or grappling). Most common within sexes but can occur between sexes
Mates	Two crickets mate, with the female mounting the male from behind, the male passing a spermatophore to the female and the spermatophore remaining fixed to the base of the female's ovipositor
Predated by XX	The cricket is killed by a predator, normally a robin (*Erithacus rubecula*) or a shrew (*Sorex araneus*)
Eclosion	A cricket sheds its last moult and becomes an adult

any kind of aggressive interaction between them (see Table 1), which can be unidirectional. These fights typically occur immediately after a cricket arrives at a burrow at which there is already a member of the same sex, and they very rarely occur between males and females. The loser will then leave the burrow. These fights are assumed to be over potential mating partners (Alexander, 1961) or to provide access to the safety of a burrow. We split the season into nine 8-day time periods, which gives a manageable number of time steps but also allows enough time for interactions to occur to prevent each time period having a low frequency of interactions. To avoid exceptionally sparse networks, we removed crickets ($N = 58$) who only fought a single other individual in a single time period, leaving networks of 108 individuals. Removing these individuals removed some of the connections of remaining individuals. In some cases, this led to an individual only having a single remaining connection. The same was true for the mating network (below). We did not continue to remove such individuals in an iterative manner, as this would have substantially reduced our sample size.

For each time period, we created a network linking individuals if they fought at least once in that time period (hence the networks were binary). If an individual was not alive during a time period, we entered 'structural zeroes' for all its potential interactions. These indicate that interactions with that individual could not have taken place, preventing the lack of interaction from informing parameter estimates (Ripley et al., 2015). A lack of interaction when both crickets were alive indicates they did not interact when they theoretically could have done, hence this observation is useful for informing parameter estimates.

For the mating network, we linked crickets in a network if they mated at least once in the 8-day period, similar to the fighting network (again a binary network). We added structural zeroes for all potential interactions between individuals of the same sex, as such interactions in that network were impossible. This was input into a SAOM alongside the networks of fighting behaviour, as we expected them to influence each other. We limited both networks to crickets who mated or fought more than one other cricket or mated or fought in more than one time period, giving networks of 113 crickets, a slightly larger subset of the population than used previously, again to prevent exceptionally sparse networks. This restriction differed from the one used above, as requiring a cricket to have both mated and to have fought more than one other cricket in more than one time period reduced the network to 58 individuals. We felt this underpowered our analysis too substantially to be acceptable, and that it was preferable to change the restriction to achieve similar sample sizes in the two analyses. For both networks, if an individual was not alive during a time period, we entered structural zeroes for all its potential interactions.

Network Analysis

Unless otherwise stated, we used the same method and rationale as outlined in Fisher et al. (2017) and that article's supplementary materials. We initially had nine 8-day time periods. However, in the first two and last two time periods there were not enough social interactions to investigate the processes that could influence their change, so we did not use them, leaving the middle five time periods (spanning 20 May 2013–28 June 2013). Terms are considered significant at the 95% if the absolute value of 'estimate/standard error' was >2 (Burk et al., 2007; Ripley et al., 2015). Below we explain the modelling process for each of the networks.

In a SAOM, the model type must be specified, as this influences the interpretation of parameters. For the fighting network we used a 'forcing' model (model type 2), where one individual dictates whether a tie is created or dissolved (Ripley et al., 2015), e.g. a cricket can simply attack another or leave the area when they both meet. The initial SAOM for fighting behaviour contained rate parameters (the frequency of the formation and dissolution of links) for each time period and the effects of 'connectivity' (the tendency for individuals to be connected to all others in the network, which is typically negative as networks are generally sparse; note that this term is referred to as 'density' in much of the SAOM literature, but we avoid that term to avoid confusion with other definitions in network analysis for 'density') and 'triadic closure' (the tendency for individuals to form connections with those they share a mutual connection with, which is typically positive as individuals interact with those they share a mutual connection with). In Table 2, we provide definitions of all terms used in our analyses and what it means for interactions in the network when those terms are positive or negative.

We tested the initial SAOM for the fighting network for satisfactory goodness of fit (GOF) with three network statistics: degree distribution (the frequencies of the different numbers of unique connections possessed by crickets in the networks), geodesic distribution (the frequencies of the different shortest path lengths in the networks) and the triad census (the frequencies of each set of three crickets that possessed 0, 1, 2 or 3 links among them, cf. Ilany et al., 2015). These were chosen as they are commonly calculated network statistics, but their values are not defined by any of the parameters in the model (Ripley et al., 2015). The observed network statistics were not different from the network statistics of the set of networks generated by the model fitting process ($P = 0.281$, 0.399 and 0.994 for the GOF tests for degree distribution, geodesic distribution and the triad census, respectively), indicating a satisfactory fit had been achieved. We therefore began adding terms of interest. After adding a term, we ran the model until it achieved convergence and assessed the GOF. If the GOF had worsened, we removed the newly added term(s) before continuing, otherwise it/they were retained (see Fisher et al., 2017, for further details).

First, we added the individual covariate of sex and two parameters, one for sex affecting the number of interactions an individual has and one for interactions occurring depending on the sex of both individuals ('sex ego × sex alter'). The former term models the tendency for members of one sex to fight more often than members of the other sex, which we expected to have little effect based on previous results (Fisher, Rodríguez-Muñoz, &

Table 2
A description of each of the different terms fitted in our two models

Effect name	Description	Positive means	Negative means
Rate of change (periods 1–4)	Relative frequency of changes in interaction partners in a given transition	Larger values indicate more changes took place	NA
Connectivity	Tendency to be connected to all other individuals	Connected with many individuals in the network	Connected with few individuals in the network
Triadic closure	Tendency to form connections with those with a mutual connection	More likely to interact if sharing a mutual contact	Less likely to interact if sharing a mutual contact
Distance	How spatial distance influences interaction chance	Farther distance increases chances of interacting	Farther distance decreases chances of interacting
Sex	How being male influences interaction probability compared to being female	Males have higher interaction probability than females	Males have lower interaction probability than females
Sex ego × sex alter	Change in interaction probability when both individuals are the same sex	Same-sex interactions are more likely than opposite-sex interactions	Same-sex interactions are less likely than opposite-sex interactions
Mass	How mass influences interaction probability	Heavier crickets have higher chance of interacting	Heavier crickets have lower chance of interacting
Mass ego × mass alter	How mass of both focal individual and potential opponent combine to influence interaction probability	Crickets of similar mass have a higher chance of interacting	Crickets of similar mass have a lower chance of interacting
Rainfall	Influence of rainfall on interaction probability	Periods with more rain have more interactions	Periods with more rain have fewer interactions
Solar radiation	Influence of solar radiation on interaction probability	Periods with more sun have more interactions	Periods with more sun have fewer interactions
Popularity in mating network	How number of connections in mating network influences interaction probability in fighting network	Many connections in mating network increase chance of interacting in fighting network	Many connections in mating network decrease chance of interacting in fighting network
Popularity in fighting network	How number of connections in fighting network influences interaction probability in mating network	Many connections in fighting network increase chance of interacting in mating network	Many connections in fighting network decrease chance of interacting in mating network
Degree assortativity	The tendency for individuals to interact with individuals of the same number of connections ('degree')	Individuals with similar numbers of connections are more likely to interact	Individuals with similar numbers of connections are less likely to interact
Mutual partner	The tendency for two individuals that fight to then be more likely to share a mutual connection in the mating network	Individuals that fight are more likely to have mated with the same individual	Individuals that fight are less likely to have mated with the same individual

We also indicate what positive or negative values of the term would mean for the interactions in the network. Note that rates of change cannot be negative.

Tregenza, 2016a, b). The latter term models the tendency for crickets to predominantly fight members of the same sex as themselves, which we expected to be a strong effect as fights between males and females are exceptionally rare. We next added a changing dyadic covariate of 'distance', which was the Euclidean distance between each pair of crickets at the end of a given time period. This models the extent to which crickets nearer each other are more likely to interact than those farther away. As a SAOM models the transitions between networks, rather than the structure of the networks themselves, we entered four instead of five measures of distance for the four transitions, with the distances at the end of the first time period informing the transition between the first and second networks, and so on. We then added the constant covariate of individual mass (g) and its effect on the number of connections an individual acquired ('mass'), and the interaction between the mass of each individual and its potential associates ('mass ego × mass alter'). We expected heavier crickets to fight more often (Dixon & Cade, 1986) and crickets to avoid fighting much heavier individuals (Arnott & Elwood, 2009). We next added two effects for weather: the total amount of rainfall (cm; 'rainfall') and the intensity of solar radiation (W/m^2; 'solar radiation') in each time period. These were predicted to increase and decrease the frequency of social interactions, respectively, as they have concurrent effects on movement around burrows (Fisher, James, Rodriguez-Munoz, & Tregenza, 2015). Each individual was scored as being exposed to the same amount of rainfall and solar radiation in each time period. Each term did not worsen the GOF of the model (not shown) and so were retained. This is the final model for the fighting network dynamics.

Mating and Fighting Networks

To simultaneously analyse mating and fighting, we entered the five mating networks alongside the five fighting networks into a SAOM. We used a 'unilateral initiative and reciprocal confirmation' model (model type 3; Ripley et al., 2015), since for mating, both crickets need to be receptive for it to occur. This model initially included the effects of connectivity and triadic closure for both networks. We removed the effect of triadic closure from the mating network, as triadic closure would be impossible in this network (as the third interaction in the triad would have to be a same-sex mating). Once this model converged, we began adding terms. The GOF for the mating network was not initially satisfactory ($P = 0.019$, 0.041 and 0.008 for the GOF tests for degree distribution, geodesic distribution and the triad census, respectively), so we added the effect of 'degree assortativity' for the mating network. If significant and positive, this effect indicates that individuals with many associations preferentially interact with other individuals with many associations. This possibly represents mutual mate choice, something we have found inferential evidence for previously (Fisher et al., 2016a). This model converged and achieved satisfactory GOF ($P = 0.413$, 0.612 and 1.00 for the GOF tests for degree distribution, geodesic distribution and the triad census, respectively), so we began adding terms to determine what contributes to the accumulation of opportunities to gain fitness.

We first added the changing dyadic covariate of distance for both networks, calculated in the same way as previously for the fighting network. We next added the effect of mass for both networks, and the interaction between the mass of two potential

associates for the mating network. The latter effect was not added for the fighting network in this two-network model, as the prior results indicated it was not important (see Results, Table 3), and we wished to avoid overparameterizing the model. We expected mass to be positively related to mating interactions, but for the interaction to not be important, as individuals of all sizes may prefer larger, presumably more fecund individuals (e.g. Aquiloni & Gherardi, 2008; Baldauf, Kullmann, Schroth, Thünken, & Bakker, 2009). We also added the effects of rainfall and solar radiation for the mating network. These were not added for the fighting network as previous results indicated they were not important (see Results, Table 3).

We then added terms relating to the coevolution between the networks. The first of these was the effect of 'across-network popularity', where an individual's number of connections in one network influences its number of connections in the other network. We actually added two effects here, one for the fighting network's effect on the mating network and then the effect in the opposite direction. While we were principally interested in the first effect, we fitted the second effect to explore the possibility that mating interactions influence fighting interactions. We expected a positive effect of fighting network connections on mating network interactions, as individuals engaging in many fights are assumed to be doing so to gain access to many mating partners. We also expected a positive effect of mating network interactions on fighting network connections, as individuals mating with many partners may then encounter many rivals to fight with. We finally added the 'mutual partner' effect from the fighting network to the mating network. This models the possibility that two individuals that fight are then more likely to share a mutual connection in the mating network. We have previously found that two males who fight are also typically in sperm competition (Fisher et al., 2016a), so we expected this effect to be positive. This was our final model.

RESULTS

Fighting Network

Plots of the fighting network at each time point and the overall distribution of the number of connections in this network are given in Fig. 1a–f. From the final model of fighting we found significant effects of connectivity, triadic closure, the spatial distance between two individuals, an individual's mass and both the main effect of sex and the interaction between the sexes of two potential associates (Table 3). The connectivity effect was strongly negative, indicating that crickets tend not to be connected to all other crickets, and so the network is relatively sparse, like most social networks (Snijders et al., 2010). Triadic closure was positive, indicating that the presence of a mutual connection increased the chances of two crickets fighting. This was true even when accounting for the effect of distance between individuals, which negatively influenced their tendency to have interactions. The sex effect was negative, indicating that males fought fewer other individuals than females, while the interaction between the sex of one cricket and the sex of another was strongly positive, indicating that fights are predominantly intrasex. Heavier crickets fought more other crickets, again as predicted, but individuals did not avoid fighting those of greatly different mass to them (the interaction between the mass of an individual and the mass of its potential fighting partner was not important). The weather variables did not influence the fighting network.

Table 3
Results for the stochastic actor-orientated models (SAOMs) for the fighting network

Effect name	Estimate	SE	Convergence	*t* statistic
Rate of change (period 1)	3.300	1.130	NA	2.921
Rate of change (period 2)	2.169	0.373	NA	5.811
Rate of change (period 3)	1.040	0.191	NA	5.456
Rate of change (period 4)	1.913	0.456	NA	4.200
Density	**-4.519**	**0.355**	**0.057**	**-12.739**
Triadic closure	**0.861**	**0.217**	**0.024**	**3.959**
Distance	**-0.159**	**0.018**	**-0.075**	**-8.790**
Sex	**-0.414**	**0.183**	**-0.031**	**-2.262**
Sex ego × sex alter	**6.398**	**1.144**	**0.059**	**5.595**
Mass	**1.991**	**0.892**	**-0.003**	**2.232**
Mass ego × mass alter	-5.214	5.466	-0.005	-0.954
Rainfall	0.007	0.013	0.058	0.592
Solar radiation	< 0.001	< 0.001	-0.025	1.500
Maximum convergence ratio = 0.118				

Shown are the effect estimates, standard errors, convergence scores and the *t* statistics (estimate / standard error). Effects are considered significant at the 95% level when the absolute *t* statistic is greater than two. Such effects (aside from the rate parameters) are highlighted in bold. Rate parameters in a SAOM with only one dependent network are calculated rather than estimated, so convergence scores are not given here. Also shown is the maximum convergence ratio for the entire model, the maximum *t* ratio for convergence for any linear combination of the parameters.

Mating and Fighting Networks

Plots of the mating network at each time point and the overall distribution of the number of connections in this network are given in Fig. 1g–l. In the SAOM for the mating and fighting networks, all the significant effects from the previous analysis of the fighting network were in the same direction as before, although the effects of sex, distance and mass were not significant (Table 4). This possibly indicates a lack of power in this analysis. The effect of across-network popularity from the mating network to the fighting network was significantly negative, indicating that individuals who mate with many others fight fewer other crickets in the next time period.

For the mating network, the connectivity effect was strongly negative as for the fighting network, again indicating the mating network is sparse much like other social networks. The effect of degree assortativity was positive, indicating that promiscuous males mated with promiscuous females. Otherwise, no effects were significant, but since there was possibly a lack of power in this analysis, we will mention the following effects that were close to significance (estimate/standard error| >1). Increasing distance decreased the likelihood of mating interactions, while rainfall increased their likelihood. The mutual partner effect was positive, suggesting that crickets that are connected in the fighting network tend to be more likely to share a mutual connection in the mating network. Neither the main effect of mass nor the interaction between mass of the male and female were important, nor was the effect of solar radiation or the effect of popularity in the fighting network.

DISCUSSION

Both our dynamic network of fighting and the dynamic network of mating were structured by nonstochastic factors, confirming our predictions. Individual mass, physical distances and the presence of mutual connections with males and females all influenced the accumulation of fighting interactions in wild crickets and led to the kind of skew in social interactions that is common to the vast majority of social networks. We were also able to recapture the skew in interactions in the mating network. A relatively simple process, the assortment of individuals by their existing number of connections, gave patterns of mating interactions that led to the kind of skew in mating success previously found in our system and commonly observed in nature. Furthermore, although we did not find that interactions in the fighting network influenced mating interactions, we did identify how interactions in the mating network influenced fighting interactions. This shows how social interactions in one context can influence the accumulation of

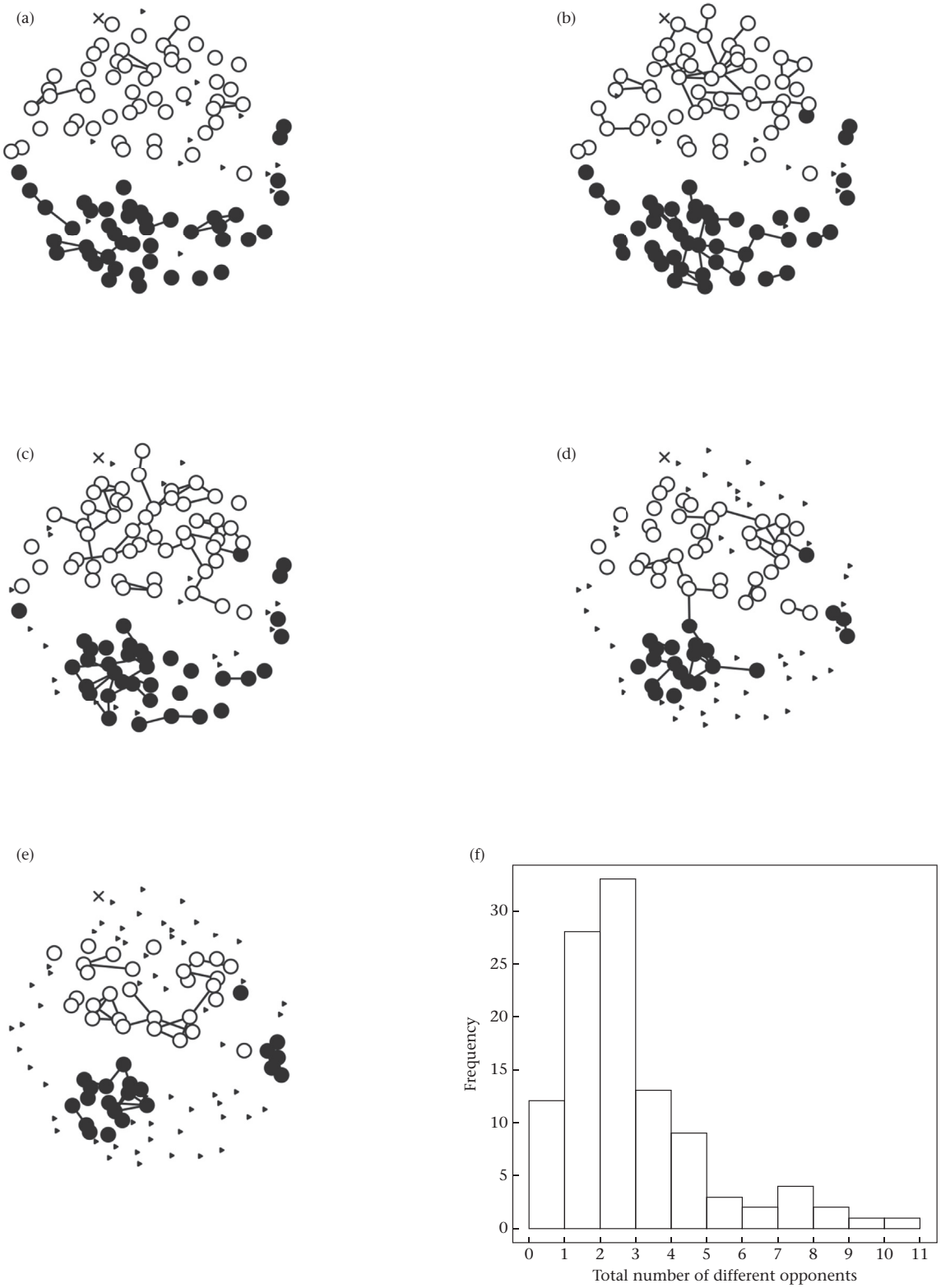

Figure 1. A network plot for each of the five time periods for the fighting network (a–e), the distribution of the different number of opponents these networks give in aggregate (f), a network plot for each of the five time periods for the mating network (g–k) and the distribution of the number of unique mating partners that these networks give in aggregate (l). For the network plots, males are filled circles, and females open circles. Individuals who were not alive during the time period are plotted as a small triangle. For g–k, the size of the circular nodes indicates the degree in the fighting network of that individual in that time period. The position of an individual is consistent within plots a–f, and within plots g–k, but not between the fighting and mating networks. Position in each type of network depends on a Fruchterman–Reingold algorithm (Fruchterman & Reingold, 1991) based on an aggregation of all five time periods. For illustrative purposes, the 'X' on plots a–f indicates a female who fought no individuals in the first time period, but fought two different individuals in the second time period and was dead from the third time period onwards. For plots g–k, the 'X' indicates a male that had no matings and no fights in the first time period, mated with one female and had two fights in the second time period, mated with two females and had one fight in the third time period and was dead from the fourth time period onwards. Networks plotted using the R package 'network' (Butts, 2008). For the distributions (f, l), all five time periods are aggregated to give the frequencies of the total number of different crickets that an individual fought (f) or mated with (l) over 40 days.

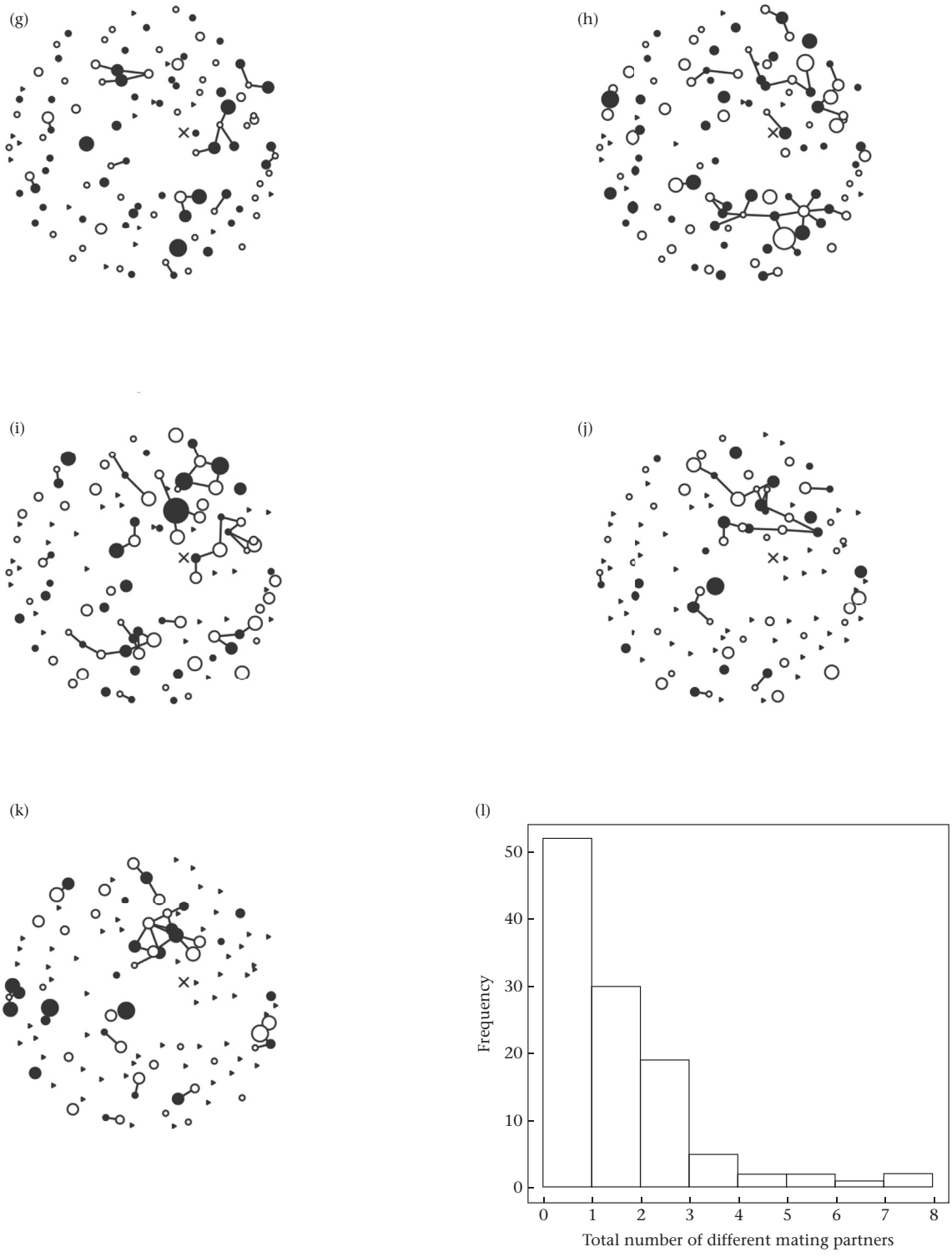

Figure 1. (*continued*).

interactions in another context. We now deal with each of our results in more detail.

Interactions in the Fighting Network

We found that males fought fewer different individuals than females (see also Fisher, Rodríguez-Muñoz, & Tregenza, 2016b). This does not necessarily mean that females are more aggressive; in this species, while both sexes engage in active mate searching (Hissmann, 1990), typically it is females that move between burrows, while males sit and sing to attract them. Females are therefore more likely to encounter several different females as they are moving among burrows, and so be involved in an aggressive interaction with them. Males may engage in repeated fights with

the same individuals, especially if they are calling from nearby burrows, which our analysis would not capture. Fighting among males does not decrease the intensity of sperm competition between them (Fisher et al., 2016a), and since fights have inevitable energetic costs and carry the risk of injury, fights may not bring sufficient sexually selected benefits for males to drive combat with many different rivals.

The effect of spatial distance was negative, as expected. In many species, individuals will associate more with those close to them, so controlling for spatial proximity when attempting to detect genuinely socially driven associations is important (Whitehead & James, 2015). However, the relationship is likely to be bidirectional for many species, with space use influencing social interactions and animals' movements based on the results or anticipated consequences of social interactions (Cantor et al., 2012; Webber & Vander Wal, 2018). This makes simply 'controlling' for space use problematic when space use itself may be an expression of social behaviour.

Heavier crickets fought more different individuals. This may suggest that fighting is a condition-dependent strategy (Luttbeg & Sih, 2010) or that heavier individuals use a different social strategy that involves attempting to dominate their rivals (Brown, Smith, Moskalik, & Gabriel, 2006; Hack, 1997). The interaction between an individual's mass and the mass of its potential associates was, however, not important. This may be because we only modelled the occurrence of fights, not who won. It may well be that crickets of different sizes will encounter each other at a burrow and interact aggressively, and then the size difference influences the outcome.

Finally, we found no link between the weather variables and formation of connections in the fighting network. We consider it unlikely that rainfall and solar radiation do not influence cricket social interactions, as crickets' activity levels on a given day are influenced by the amount of rain and solar radiation (Fisher et al., 2015). Instead, we suspect that the 8-day periods we selected were too coarse a scale to detect these fine-scale behavioural responses. Ilany et al. (2015) found that wetter years lead to more sparse social networks in spotted hyaenas, *Crocuta crocuta*, using a SAOM, so relationships between environmental and network characteristics can be detected with this approach in some systems.

Interactions in the Mating Network

We found that a relatively simple process, where successful individuals (those with many connections in the mating network) mate with other successful individuals, leads to a highly skewed pattern of mating success. Reproductive skew is ubiquitous in natural populations (Clutton-Brock et al., 1997; Engh, 2002; Frentiu & Chenoweth, 2008; Keller & Reeve, 1994; Rodríguez-Muñoz et al., 2010; Ryder et al., 2009; Thompson et al., 2011) and provides the variation in fitness necessary for adaptation. It would be interesting to know the extent to which other mating systems can be modelled in this manner and whether the process of degree assortativity is as important in other mating systems as it is in crickets.

Assortment by promiscuity (as we have shown here) may indicate mutual mate choice or assortment by 'quality' (Aquiloni & Gherardi, 2008; Baldauf et al., 2009), which could increase the variance in reproductive success in the population if high-fecundity individuals pair. However, as males with many mating partners mate with more promiscuous females, they face increased sperm competition for each ovum of females they mate with. This will reduce the variance in reproductive success among males (Sih, Hanser, & McHugh, 2009). Both the main effect of mass and the interaction between the mass of an individual and the mass of its potential mating partners was not related to links in the mating network, suggesting that mating partner choice is not based on mass. Instead, chemical cues such as cuticular hydrocarbons are likely to be important in mediating partner choice between closely related species (Tyler, Fisher, D'Ettorre, Rodriguez-Munoz, & Tregenza, 2015), so may play a role here.

Only degree assortativity was needed to get a satisfactory GOF for the mating network, perhaps suggesting that the mating system is quite simple and, beyond this term, only stochasticity plays an additional role in determining its structure. This would be troubling given the amount of effort that is devoted to understanding patterns of mate choice and sexual selection in the wild. However, there is the potential for a lot of different behavioural processes to be contained within the effect of degree assortativity, such as the trait(s) crickets use for mate choice and the processes that generate variation in these traits that cannot be exploited by 'cheats' who do not signal honestly. Additionally, we have only modelled the choice of mating partners, not the frequency of mating with a particular partner in an 8-day period, as we used binary networks. Therefore, there is probably variation in preference among mating partners that we are ignoring, which could influence fitness, as frequency of copulation is probably related to share of paternity (Parker, 1970; Simmons, 1987).

We found that spatial distance did not significantly influence the mating network. This surprising result could stem from a number of sources. A lack of power as suggested earlier may have prevented us from detecting a biologically important effect. Alternatively, this may reflect the fact that there are many crickets near each other that do not mate. In general, if the choice of mates for an individual in a population is not limited to its immediate neighbours, simple models for population-level processes such as partner choice or sexual disease transmission that do not explicitly account for spatial constraints may be more accurate than thought (Patterson, Thomas, Wilcox, Ovaskainen, & Matthiopoulos, 2008). The weather variables were also not important, but we hesitate to make conclusions about this since it may stem from looking at too coarse a scale as suggested above for the fighting network.

Individuals with more mating partners tended to have fewer fighting partners at the next time step. We did not predict this effect; we expected there to be a positive relationship between the number of fighting partners and the number of mating partners. Furthermore, this seems to contrast with previous results that the involvement in fighting and sperm competition is positively correlated (Fisher et al., 2016a). However, these results are compatible if we consider the dynamic nature of the new result. Crickets over their lifetimes may show positive correlations between involvement in different types of competition, perhaps due to links to 'quality' or differences in life span, but at any given time they may not be able do both (perhaps due to energetic constraints), creating a negative relationship between adjacent time steps. Furthermore, crickets that shared a mutual connection in the mating network were more likely to fight. This seems a direct response to the threat of sperm competition, as we have found previously (Fisher et al., 2016a). Crickets have flexible mating systems where they are involved in pre- and post-copulatory competition (Buzatto, Tomkins, & Simmons, 2014), so they are adapted to both physical contests and sperm competition. In other systems, where males can monopolize access to females through physical domination, we would not expect to see such a pattern. The nuances of social interactions in various forms, such as mating and fighting, may be more thoroughly explored through 'multilayer' network analysis (Finn, Silk, Porter, & Pinter-Wollman, 2019; Silk, Finn, Porter, & Pinter-Wollman, 2018); what we have shown here is that the links between contests and mating interactions play a role in the dynamic change of a social network.

Table 4
Results for the stochastic actor-orientated models (SAOMs) of the mating and fighting network

	Estimate	Standard error	Convergence	*t* statistic
Fighting network effects				
Rate of change (period 1)	3.300	NA	NA	NA
Rate of change (period 2)	2.169	NA	NA	NA
Rate of change (period 3)	1.040	NA	NA	NA
Rate of change (period 4)	1.913	NA	NA	NA
Density	**-2.004**	**0.170**	**-0.067**	**-11.795**
Triadic closure	**0.862**	**0.221**	**-0.026**	**3.907**
Distance	-0.005	0.016	0.072	-0.313
Sex	-0.129	0.135	0.030	-0.955
Sex ego × sex alter	**3.270**	**0.577**	**-0.076**	**5.672**
Mass	0.997	0.714	0.056	1.396
Popularity in mating network	**-0.637**	**0.291**	**0.027**	**-2.185**
Mating network effects				
Rate of change (period 1)	5.306	1.490	0.015	3.558
Rate of change (period 2)	3.829	1.018	-0.009	3.761
Rate of change (period 3)	3.280	0.894	0.013	3.669
Rate of change (period 4)	3.664	1.657	0.007	2.212
Density	**-1.605**	**0.118**	**-0.002**	**-13.609**
Degree assortativity	**0.158**	**0.066**	**-0.004**	**2.411**
Distance	-0.019	0.017	0.004	-1.139
Mass	-0.610	0.715	-0.033	-0.853
Mass ego × mass alter	-1.704	4.520	-0.019	-0.377
Rainfall	0.011	0.007	-0.028	1.454
Solar radiation	< 0.001	< 0.001	0.001	0.343
Popularity in fighting network	-0.026	0.185	-0.033	-0.138
Mutual partner	1.143	0.838	-0.009	1.364
Maximum convergence ratio = 0.146				

Shown are the effect estimates, standard errors, convergence scores and the *t* statistics (estimate and standard error). Effects are considered significant at the 95% level when the absolute *t* statistic is greater than two. Such effects (aside from the rate parameters) are highlighted in bold. The four rate-of-change parameters for the fighting network were fixed rather than freely estimated, hence their statistics other than the estimate are not provided (see Table 2 for these estimates). Also shown is the maximum convergence ratio for the entire model, the maximum *t* ratio for convergence for any linear combination of the parameters.

Conclusions

We have analysed how networks of fighting and mating interactions between crickets accumulate over time, and therefore arrived at a holistic understanding of how these networks come to be structured. By demonstrating that various individual- and network-based factors influence social interactions, we have helped link social network analysis to existing theory on dominance interactions and sexual selection theory. These factors, along with unmodelled processes, produced networks with a skewed degree distribution that mirrors the observed skew in social interactions and reproductive success in the population. This demonstrates that a dynamic network approach may be a good way to model the accumulation of mating opportunities that give rise to strong skews in fitness in wild populations. We hope this stimulates others to use approaches such as this to gain more complete understanding of complex animal social systems.

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